

Conference Paper

Functional Organization of the Brain and Psychic Activity: A View Beyond Luria (With Luria)

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Abstract

This paper reviews, elaborates, and rebuilds Luria's model of the three functional units of the brain. As a result, five functional brain units have been delineated: preferential (unit for life-support and arousal regulation), limbic (unit for valuation/motivation and for context memory), cortical and thalamic-cortical ("the conscious agent"), basal ganglia ("the reinforcer"), and cerebellar ("the supervisor"). The new model is more realistic; it includes elements missing from Luria's model and avoids a corticocentric approach. It will allow a better analysis of the effects of brain pathology on cognition, neuropsychiatry, and behavior. Within the framework, the concept of complex functional system is maintained and expanded.

Keywords: brain, functional model, complex systems, cortex, Luria.

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1. Introduction

Aleksandr Romanovich Luria is one of the greatest authorities in the history and configuration of current neuropsychology. The world's scientific community recognizes his theoretical concepts [25]. Luria (1973) considered the existence of solid grounds for *"distinguishing three main functional units of the brain whose participation is necessary for any type of mental activity"* [English ed. p. 43]). He wrote: *"they can be described as a unit for regulating tone or waking, a unit for obtaining, processing and storing information coming from the outside world, and a unit for programming, regulating and verifying mental activity"* [p. 43]. These units were located in specific brain structures. Unit I: brain stem, diencephalon, and mesial regions of the cortex. Unit II: *"lateral regions of the neocortex on the convex surface of the hemispheres, of which it occupies the posterior regions, including the visual (occipital), auditory (temporal), and general sensory (parietal) regions"* [p. 67]. Unit III: *"anterior regions of the hemispheres, anteriorly to the precentral gyrus"* [p.80]. As proposed by Luria (1973), mental functions are organized into systems

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of concertedly working zones, each of which performs its role, and which may be located in completely different and often far distant areas of the brain. Luria (1973) also recognized “*the principle of vertical organization of all structures of the brain*” [p. 46].

Luria’s model has been the subject of a large number of papers. Years ago, the need to carry out a series of revisions of the three-block model had already raised [25, 30]. The objective of this paper is to develop Luria’s model of the three functional units.

2. Methodology

A search of published medical literature on the subject was carried out. It was initially *ad hoc*, in books on neuropsychology, behavioral neurology, neuroscience, and neuropsychiatry. A specific PubMed search was performed in the fields of phylogeny, anatomy, physiology and neuroimaging.

3. Results

3.1. Guidelines for the development of a new functional brain model

The following simplified guidelines (considerations, additions, and differentiations) were considered to build an updated new functional model:

1. A functional model requires a multilevel analysis of the nervous organization. In this regard, “*any given behavior of an organism depends on a hierarchy of levels of organization*” ([28], p.6) (from molecules to systems of behavior). Local canonical circuits have a functional specificity that explains part of their contribution to large-scale processing. It must be recognized that the biological foundations of cognitive abilities and behavior are not corticocentric [23].
2. It is interesting to highlight Yakovlev’s (1948) model concerning telencephalon *impar* (rhinal), *semipar* (limbic), and *totopar* (supralimbic). It agrees with the anatomical and histological descriptions of Mesulam (2000): limbic areas (cortical + allocortex), paralimbic areas, homotypical isocortex (high order heteromodal, and modality specific isocortex), and idiosyncratic cortex. Such an approach allows the recognition of three large groups of structures: medial, limbic and supralimbic.

3. Anokhin's (1935) concept of "functional systems" (FS), and "complex functional systems" (CFS) permits the unification of the individual (local) mechanisms of the organism into an integral system for adaptive behavior (creation of an "integrating unit"). Two types of FS have been described. FS Type I provide homeostasis due to internal resources of the body, inside its boundaries (e.g. blood pressure control). FS Type II support homeostasis due to a changes of behavior (interaction with the outside world) and are the basis of different types of behavior [20].
4. The model must include the concept of "value" (biological, cultural) and its measurement, which is related to the reward/motivation systems [7]. The FS responsible for behavior *"must rank on a priority scale all motivations simultaneously present according to their urgency and that, to achieve such a ranking, the system must choose among competing motives based on a common currency"* (Cabanac, p. 117). These systems constitute the "behavioral final common path" of the brain [21].
5. When the brainstem is studied, it is necessary to include the neuromodulatory neurotransmitter systems and the specific function of the dopaminergic systems [3]. The inclusion of cranial nerve nuclei located in the brainstem is also required. Cranial nerves play a key role in the management of specific afferences, and in the expression of voluntary (e.g., language), autonomic, and emotional behaviors.
6. A comprehensive model requires the inclusion of autonomic systems, as part of the homeostasis control [3]. Depending on the hedonic and emotional value of the stimuli, the autonomic responses are very different ("fight or fly" versus "rest and digest") [3].
7. For the new model to be more comprehensive, the role of the limbic system must be differentiated. The limbic system has two main structures: amygdala and hippocampal formation (HF) [22]. These structures are related to the brainstem, the hypothalamus, and the paralimbic cortex.
8. The anatomical and functional division of the cortex is another fundamental issue. As Luria (1973) did, it is possible to recognize an anterior-posterior division although it presents many limitations. The process of *"obtaining, processing and storing information coming from the outside world"*, does not depend exclusively on the posterior cortex [14, 19, 26]. For this reason, it is crucial to avoid the anterior-posterior dichotomy, and to unify the supralimbic cortex into a single functional unit. The neural underpinnings of language and semantic cognition must be reconsidered (see [10]).

9. The model should include the role of connection pathways of the brain (hodology) [5]: intrahemispheric and interhemispheric pathways (see [6]). Finally, it is essential to incorporate the concepts of structural and functional connectome (see [16, 29, 34]).
10. It is necessary to recognize the functional role of the thalamus beyond a relay center. The thalamus is an integrating center in functional brain networks (see [15]).
11. The specific functional role of the basal ganglia should be included in the model [35]. The basal ganglia are an old system of vertical control of behavior. They plays a major part in action selection within the context of an actor-critic model [9].
12. A new comprehensive brain model should include the specific role of the cerebellum in neuropsychological functions. The cerebellar function is beyond motor control [18, 27].
13. An advanced model should be comprised of types of learning (unsupervised, reinforcement, supervised) (see [9]) and memory processing (see [13]), their neural bases and their relationships.
14. The new model should contain concepts of social neuroscience and major functional aspects such as empathy, and theory of mind (see [11]). Concomitantly, it should consider the biological basis of psychiatric and neuropsychiatric syndromes (see [12]).
15. The model must incorporate the physiological and computational role of cortical rhythms and oscillatory cerebral dynamics [31]. It must also raise the problem of synchronization of distributed CFS and the issues of consciousness, self-awareness, and orientation (see [8, 24, 32]).

3.2. Development and definition of a new functional brain model: five units

The functional units considered in this proposal are shown in Table 1. The model is characterized by the following elements: Luria's unit I is maintained in an expanded form (new components are included). A limbic unit (II) is differentiated, in which two components are recognized (amygdala-paleocortex and hippocampus-archicortex). Luria's units II and III are unified into a single unit (III). Two new units are added: basal ganglia

systems (IV), and cerebellar systems (V) which recognize the vertically organized re-entrant systems of the brain (see [17]).

TABLE 1: A brain model of five functional units.

Systems (Units)	Main Neural structures	Main Functions
I. Preferential systems	<ul style="list-style-type: none"> •Reticular systems •Ascending neuromodulatory systems •Hypothalamus •Autonomic systems •Nuclei of the cranial nerves 	<i>Life-support & arousal regulation</i> <ul style="list-style-type: none"> •Homeostasis •Autonomic control •Arousal & attention •Behavior modulation
II. Core limbic systems	<ul style="list-style-type: none"> •Olfactory division •Amygdalocentric division •Hippocampocentric division 	<i>Valuation/motivation & context memory</i> <ul style="list-style-type: none"> •Hedonic axis. Emotion •Context and memory processing
III. Cortical & thalamic-cortical systems	<ul style="list-style-type: none"> •Supralimbic cortex •Thalamic-cortical pathways •Cortico-cortical connections: intra & interhemispheric 	<i>"The conscious agent"</i> <ul style="list-style-type: none"> •Associations (internal & external spaces) •Behavioral final common path •Unsupervised learning
IV. Basal ganglia systems	<ul style="list-style-type: none"> •Limbic/paralimbic division •Associative division •Sensorimotor division 	<i>"The reinforcer"</i> <ul style="list-style-type: none"> •Reward systems •Behavior selection & control •Reinforcement learning
V. Cerebellar systems	<ul style="list-style-type: none"> •Limbic/paralimbic division •Associative division •Sensorimotor division 	<i>"The supervisor"</i> <ul style="list-style-type: none"> •Orthometric behavior modulation •Supervised learning

3.2.1. Unit I: preferential or primordial systems (life-support and arousal regulation)

This unit is composed of the most primitive and medial structures of the brain. It is related to homeostasis, autonomic regulation, arousal, attention, and life-support. The main brain structures that make up this unit are the following: (1) reticular formation systems; (2) ascending neuromodulatory systems (norepinephrine, dopamine, serotonin, histamine, acetylcholine); (3) nuclei of the cranial nerves; (4) hypothalamus; and (5) autonomic systems. These systems are preferential or primordial due to their functional priority based on participation in life-support processes.

The machinery of homeostasis has been designed to protect the integrity of living organisms ([7], p. 212]. The states close to the homeostatic range (desired physiological parameters) have more “value” than the deviated ones. The values attributed to objects and activities have some relation, direct or indirect, to the maintenance of living organisms within a homeostatic range. Values are intimately related to primitive systems of reward/motivation and emotions. Phylogenetically, the limbic system (unit II) is strongly interconnected with homeostatic regulation systems [20]. The hypothalamus (e.g. paraventricular nucleus [as overlapping structure]) plays a role in physiological interconnection with the amygdala, the hippocampus, and the autonomic systems. Within this broad context, the interaction between CFS type I (internal) and type II (behavioral) is critical (see below). The ascending activating and neuromodulator systems are fundamental in the activation of type II CFS. The specific function of primitive dopaminergic systems (mesostriatal [nigrostriatal], mesolimbic, and mesocortical) is crucial for motor, emotional, and cognitive functions (see unit IV).

Wakefulness (supported by structures in the brainstem) describes the state of arousal or the potential to experience awareness [8, 24]. After Luria, the main sources of reticular activation are the metabolic and instinctive processes, the arrival of stimuli from the outside world, and the *“intentions and plans, by forecasts and programs that are formed during the conscious life of man, which are social in their motivation”* ([20], p. 57 English ed.).

3.2.2. Unit II: core limbic systems (valuation/motivation and context memory)

Although Luria discussed the functional role of the paleocortical and archicortical structures, and commented on the significance of Klüver and Bucy, and Bechterev-Korsakov syndromes [20], he did not differentiate a limbic unit. This unit is practically equivalent to Yakovlev’s telencephalon semipar. It includes the limbic areas (corticoid + allocortex [paleocortex and archicortex]). Limbic structures have three main functions: olfaction (piriform cortex), declarative context memory (HF), and emotions and drives (amygdala) [22].

Physiologically, emotions are not separable from the autonomic systems (unit I). The amygdala receives information from the sensory cortices (high-resolution information), and from the thalamus (low-resolution information) [12]. The amygdala acts

as an emotional hub and contributes to reward/motivation processing. It sends efferences to the hypothalamus (hypothalamic-pituitary-adrenal axis activation), brain-stem (sympathetic arousal), substantia innominata (alertness), insula (interoception, pain), hippocampal formation (contextual memory), and to the prefrontal cortex (PFC) (attention, cognition). The PFC regulates the function of the amygdala (inhibition) [12].

The HF receives reciprocal information from (1) sensory association areas (integration of multiple sources and information modalities), and (2) the dorsolateral PFC (executive control) (Blumenfeld, 2010). The dorsolateral PFC is modulated by dopaminergic mesencephalic afferents. The HF is related to the context information (where?, when?, what?, who?) of the lived experiences. Thanks to its particular functional organization, the HF combines all contextual information [12].

The connections of the hippocampus with the ventral striatum (VS) contribute to the learning of the contexts in which a specific motivation is satisfied, through a specific behavior. When the context reappears, the FH contributes to the opening of the ventral striatum. This gate will activate, on the one hand the dorsal striatum/pallidum (towards the thalamus and the motor cortex) and, on the other hand, the ventral pallidum. In addition, the VS will activate the hypothalamic function [12].

In summary, beyond the olfactory function, the limbic system has two divisions intimately (broadband) linked: amydalocentric and hippocampocentric. The former is mainly related to emotions and feelings ("the hedonic axis" [usefulness of the stimuli = motivational capability of consciousness = useful behaviors]) [4] and vegetative states, whilst the latter is principally concerned with context (episodic) memories ("the contextualizer"). Episodic memory is based on functional relationships between the hippocampus and the neocortex [13].

3.2.3. Unit III: cortical and thalamic-cortical systems ("the conscious agent")

This unit includes the supralimbic cerebral cortex (paralimbic [mesocortex], unimodal, heteromodal, and idiosyncratic cortices), the related thalamic systems, and cortico-cortical pathways (intra- and interhemispheric association). There are five major paralimbic areas in the human brain: (1) the orbitofrontal cortex; (2) the insula; (3) the temporal pole; (4) the parahippocampal cortices; and (5) the cingulate complex [22]. Unit III is related to the associative global processing of circulating momentary brain information, the establishment of flexible CFS, and the final behavioral output. Unsupervised learning consists of the concise representation of sensory state, context, and

actions that finds appropriate modular architecture for a given task [9]. The neocortex is related to semantic memory, episodic memory [with the hippocampus], and priming [13].

Seven coarse patterns of functional connectivity (networks) have been described within the human brain: (1) visual, (2) somatomotor, (3) dorsal attention, (4) ventral attention, (5) limbic, (6) frontoparietal, and (7) default [34]. The neuroanatomy and connectivity of these brain networks, which includes vertical connections with the basal ganglia and cerebellum, are crucial to delineate a functional brain model. The default network includes the medial PFC, temporoparietal junction, lateral temporal cortex, posterior cingulate cortex, and inferior frontal gyrus. This network is linked to various modes of self-generated thought, consciousness and mental orientation in person, space, and time [24].

Distributed supralimbic brain areas form large-scale networks that present complex patterns of convergent and divergent connectivity. Within the sensory and motor cortices, functional connectivity shows topographic hierarchical representations across adjacent areas. In contrast, the association cortex is made up of networks of widely distributed and densely interconnected areas without a rigid hierarchical organization [34]. Large-scale networks may function as partially isolated modules and many association areas belong to at least two networks. As a paradigm of interactions, the precuneus, lateral temporal cortex, medial PFC, and posterior parietal cortices participate in multiple paralimbic networks that together comprise subsystems of the default mode network [34].

The mammalian brain has been conceptualized as a thalamocortical system. Thalamocortical projections relay nearly all incoming information to the cortex as well as mediate cortico-cortical relationships ([23], Blummenfeld, 2010; [15]). The thalamus is engaged by tasks requiring multiple cognitive functions. Most thalamic subdivisions show network properties that are capable of integrating multimodal information across diverse functional networks [15]. Local cortical areas, with their connections, perform their differentiated role within the context of complex functional systems. Thanks to the connection pathways, local brain processes build the basis of synthetic mental activities. Restricted cortical lesions will give rise to symptoms depending on the type and modality of local processing. As it is important to avoid Luria's anterior-posterior anatomical dichotomy, his view on the neural underpinnings of language and semantic cognition must be updated (see [10, 19, 26]).

The unimodal and heteromodal cortices are most closely involved in perceptual and motor processing, whereas the paralimbic belt plays a critical role in processing

emotion and motivation to behaviorally relevant acts, mental processing, and external events. Associative and paralimbic cortices are intercalated between the limbic areas and the primary cortices. These intercalated cortices provide links between the internal states (physiology states, drive, emotion, and autonomic function) and external spaces (multiple sensory information from the external world) [22].

The linkage between global states (internal and external) and behavioral and motor systems generates a state-action code [9]. The biological internal needs may be discharged according to the opportunities and restrictions of the external environment [22] in which the behaving individual ("the agent") is located. The final probabilistic computation that drives the agent's behavior (policy) is guided by reward signals encoded in the dopaminergic systems (see below, "the reinforcer").

3.2.4. Unit IV: cortico-striatal (basal ganglia) systems ("the reinforcer")

This unit includes the striatal-cortical systems, whose output is added to the thalamo-cortical pathways. The simplified canonical basal ganglia (BG) circuit is the following: cortex - striatum - pallidum - thalamus - cortex [3]. The BG perform a process of selective disinhibition on the thalamus (Koziol & Budding, 2008), and are specialized for procedural memory and reinforcement learning [13]. Reinforcement learning is guided by the reward signal encoded in the dopaminergic input from the substantia nigra and the ventral tegmental area [9].

Cortico-striatal systems can be highly simplified into three divisions (networks): (1) limbic, (2) associative, and (3) sensorimotor [35]. These three networks are related, respectively, with motivation/value, thought (problem solving) and movement. They form an integrated cortical-subcortical system of behavioral selection.

The **limbic network** includes the orbital and ventral PFC, the limbic (ventral) striatum (nucleus accumbens), the ventral pallidum, and the mediodorsal thalamus. It is associated with situations of stimulus-outcome (S-O), as in the case of emotions and conditioned learning [35]. The ventral striatum acts as a motivation-action gate [12].

The **associative network** includes the prefrontal, parietal, and temporal association cortices, the associative striatum (caudate/dorsomedial striatum), the associative pallidus, and the mediodorsal/ventral thalamus [35]. It is associated with novelty and executive actions. In Luria's words, *"when the subject has an appropriate motive which makes the task urgent .../... and when is confronted by a situation for which he has no ready-made (inborn or habitual) solution"* (1973, p. 327, English ed.). Novelty implies action-outcome (A-O) contingencies [35]. Successful problem solving requires

determining a synthesis of environmental information (afferent synthesis) [1] and searching for the individual operations (S-R, see below) which will be used to obtain the necessary results (outcome). Executive cognition requires keeping informative units active for relatively short periods (working memory). This online information is necessary while the task is running. This functional situation also requires attentional components and the inhibition of irrelevant automatic responses [20].

The **sensorimotor network** includes the sensorimotor cortices, the sensorimotor striatum (putamen/dorsolateral striatum), and the ventral thalamus [35]. It is associated with situations of stimulus-response (S-R) and habit formation. The stimulus (internal or external), triggers the appropriate response [17].

The gestures (praxis) are motor sequences that have been automated and categorized. They carry a meaning or an established manipulative result. As Luria (1973) recognized, during the development, and in the case of learning processes, a dynamic change of cerebral anatomical location occurs. The associative-executive system (Goal, A-O) is replaced by the sensorimotor systems (S-R).

Traditionally, a verbal-manipulative hemispheric functional differentiation has been established, a dichotomy that should be replaced by the principle of novelty-routinization [17]. The left hemisphere preferentially processes highly predictable and frequent information. Routinization allows the application of established response patterns (S-R) (e.g. praxis, automatic aspects of language), while novelty implies the activation of associative systems (A-O).

Social cognition [11] is based on the same systems and principles. For familiar and well-known situations, automatic systems are activated, while in novelty situations, associative systems must be activated [17]. Empathy (the ability to share the feelings of others), and theory of mind (the ability to infer and represent beliefs and desires), are also part of a complex neural system based on the same principles.

3.2.5. Unit V: cerebellar systems ("the supervisor")

Unit V includes the cerebellar systems. The simplified canonical cortico-cerebellar circuit is the following: cortex - pons - cerebellar cortex/dentate nucleus - red nucleus - thalamus - cortex [35]. Unlike the cerebral cortex, the cerebellar cortex shows a histological homogeneity (a single type of canonical circuit) [28]. This fact implies that it only performs one operation. This same operation will be applied to motor, cognitive, or limbic activities (emotional or autonomic). The cerebellum has a function as a "predictor or anticipator" (informing the cerebral cortex about the predicted outcome)

[17], and can be defined as a “supervised learning system” [9]. The cerebellum is also related to classical conditioning [13].

The same concept of motor dysmetria observed in cases of cerebellar lesions is applicable to cognition and emotion [27]. Consequently, it is possible to recognize that the cerebellum has an orthometric physiological function. Orthometry involves the regulation and improvement of quality, efficiency, fluidity, intensity, softness and, finally, the adaptability of motor, cognitive, behavioral, and emotional acts. The “cerebellar cognitive affective syndrome” is the diagnostic term applied to cognitive, emotional, and behavioral symptoms that appear in patients with involvement of the cerebellum. Within this context, the vermal region has been referred to as the “limbic cerebellum”, and focal involvement in this area has been related to disturbances in emotional responsiveness, alterations in personality, as well as psychotic and behavioral disturbances [18, 27].

3.3. Interactions and global function

As recognized by Luria, the interaction between the parts of the central nervous system is critical. The striatal (unit IV) and cerebellar (unit V) systems were developed in parallel with the cortex (unit III), markedly increasing -by exaptation- the available number of control processors in parallel. Evolution shows, for example, the parallel increase in the size of the frontal lobes, the inferior parietal lobe, the basal ganglia, and the cerebellum. It is impossible to understand cortical function without the specific involvement of these structures [23]. The function of the preferential unit (I) is intimately related, through broadband routes, to the limbic system [3]. The ascending reticular and neurotransmitter systems of the brainstem (unit I) access the cortex directly or indirectly, playing a crucial “waking” and modulating role. Wakefulness is crucial for awareness. For practical purposes, consciousness is often described as having two main components: awareness and wakefulness. Awareness refers to the phenomenal perception of self and surroundings, and the subjective character of experience [8]. Studies have shown that there is a decrease in functional connectivity related to the loss of consciousness. Such a decrease is distributed primarily in the posterior cingulate/precuneus, medial PFC, and lateral parietal cortex [24, 32].

Probably, one of the keys to understanding brain function is the interaction between the global associations (the “state”) made by the cortex with vertically organized systems (striatal and cerebellar systems). In fact, distributed brain systems are organized to facilitate both serial and parallel processing. Units IV (basal ganglia) and V

(cerebellar) are two vertically re-entrant brain systems, because their circuits form a loop that re-enters a cortical region near its point of origin [17]. In fact, the cortex is actually driven by basal ganglia and cerebellar input.

Synchronous rhythms represent a core mechanism for sculpting temporal coordination of neural activity in the brainwide network [31]. An important distinction concerns the difference between structural and functional brain networks. The former are defined from anatomical data sets whilst the latter are derived from neural recordings and represent their statistical relationships. Functional networks undergo rapid changes in the course of both spontaneous and task-evoked neural activity [29].

Finally, it should be remembered that brain models must be open to cultural neuroscience [2].

3.4. Limitations of the study

The proposed functional brain model is based on multiple sources of data, especially empirical ones. Nevertheless, as a model it must be open to changes based on new contributions from the neurosciences. Whilst a model tries to fit all the data into a single scheme it cannot be exhaustive [10]. In the present study, neuronal and sub-neuronal levels have not been considered. The relationships of the model with psychological and neuropsychiatric disorders deserve a specific study. Space limitation does not allow more details to be discussed in this paper.

4. Conclusions

The proposed model goes beyond Luria's view. It includes elements that are missing from his model and avoids a corticocentric approach. Five functional brain blocks (systems) are recognized: preferential, limbic, cortical/thalamic-cortical, basal ganglia, and cerebellar. The proposed model is more realistic than that of the three blocks of Luria and will allow a better analysis of the neuropsychological symptoms and their anatomical relationships. Within the framework of this new model, the concept of "complex functional system" is maintained and expanded.

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